self. He wrote to me (letter of 27 April 1959) : "Since my *Setaria* paper appeared in Brittonia specimens have been sent to me by taxonomists from three different states in which the five quantitative characteristics fit *faberii,* but the leaves were glabrous. Each person indicated they found only one or two plants of the glabrous type in a population of hairy ones." — JOSEPH MONACHINO, NEW YORK BOTANICAL GARDEN.

AN INTERPRETATION OF TWO FORMS OF OSMUNDA CINNAMOMEA

TAYLOR A. STEEVES

Within the range of Gray's Manual, six aberrant forms of the cinnamon fern, *Osmunda cinnamomea* L., have been described, in addition to the typical form and the well defined var. *glandulosa* Waters. Other varieties are also known from tropical and sub-tropical America and from eastern Asia. The writer and several of his colleagues have been interested in this species for over ten years as a remarkably fine subject for morphogenetic studies. During this period many observations have been made on plants growing under natural conditions in the vicinity of Boston, Massachusetts, and certain tagged plants have been examined in successive growing seasons. These studies have made it possible to offer at least partial explanations for two of the described forms, forma *frondosa* (T. & G.) Britt., and forma *latipinnula* Blake.

O. cinnamomea, f. *frondosa* was first described as a variety by Torrey and Gray (Torrey, 1840), and later reduced to a form by Britton (1890). In contrast to the typical condition in which fertile fronds are completely distinct from foliage fronds and are without laminar development, this form is characterized by reproductive fronds which bear some laminar tissue. In fact, sterile pinnae may predominate, with only a few sporangia-bearing leaflets present. The fertile and sterile pinnae are variously intermixed; and sometimes sporangia may even be born on the edges or backs of leafy pinnae. In the writer's own observations, the sterile pinnae have been basally located and have given way, with various intermediates, to fertile pinnae in

the upper portion of the frond in the manner reported in the original description of the phenomenon (Torry, 1840). Other arrangements, however, can occur (Kittredge, 1941). There have been well-documented suggestions that this form represents a response to unusual environmental conditions such as burning (McLouth, 1897), a late spring frost (Owen, 1901), or the close proximity of a recently tarred roadway (House, 1933); but still the form with its Latin name has persisted.

It is evident from regular observations of tagged plants in the field, that there is considerable variation from year to year in the number of fertile fronds produced by any given plant. For example, one group of 19 plants, which was treated as a unit, produced a total of four fertile fronds in 1949, and in 1950 produced 25. Although fertile fronds are not evident above ground until early spring, it is known (Steeves and Wetmore, 1953) that the nature of the leaves is fully determined within the apical bud during the preceding season. Dissections in late summer show that the fertile fronds for the next year are fully formed, but coiled, and that the sporangia are present. It would seem reasonable to suppose that environmental conditions during the period of frond determination might influence the extent of fertility in any plant. No real evidence is available on this matter, but two observations may be reported. It has been noted that a hot dry summer is usually followed by a high degree of fertility in the following spring, whereas a cooler, moister summer leads to reduced fertility. Further, a comparison made in one area between plants in heavy woods and plants in a powerline right-of-way revealed a consistently higher level of fertility in the open right-of-way. Such observations suggest that temperature, soil moisture, or possibly total light energy received might be important factors in regulating the extent of fertility. Recent studies (Sussex and Steeves, 1958) on excised leaves of several species of ferns, including *O. cinnamomea,* growing in sterile nutrient culture, have shown that an increased supply of carbohydrate favors the initiation of sporangia; but it is difficult to correlate such observations with environmental conditions in the field.

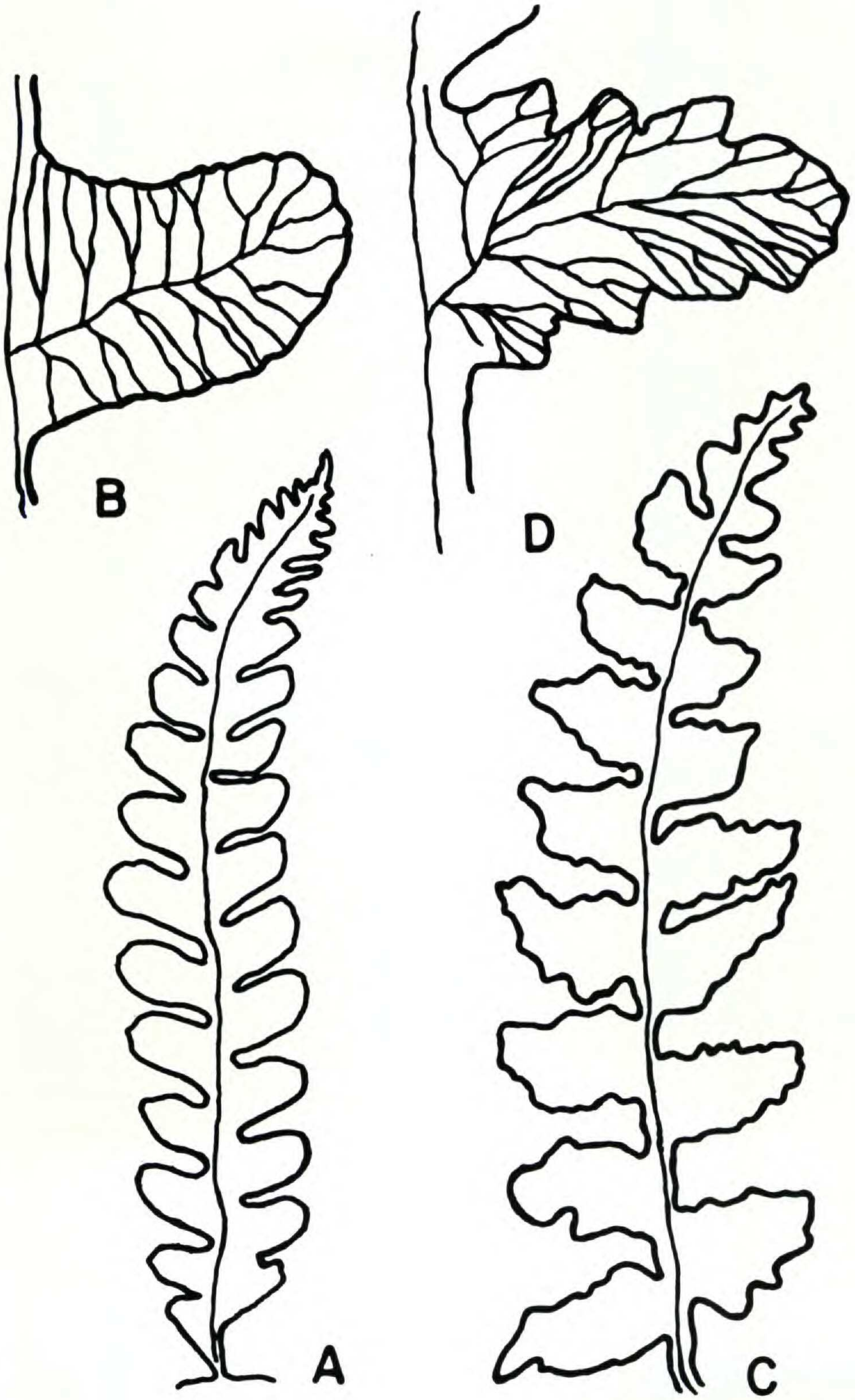

FIG. 1. A comparison of single pinnae (A and C) and single pinnules (B and D) from a typical example of *O. cinnamomea* (A and B) and from an example of *O. cinnamomea* f. *latipinnula* (C and D). A and C natural size. B and D X 4.

In the spring of 1949, the plants of the group mentioned above were all normal, that is, no mixed fertile and sterile fronds were observed. In 1950 three such fronds were found among the 25 fertile fronds produced, two on one plant, which also bore two normal fertile leaves, and one on another plant which also bore a normal fertile frond. A search of the neighboring woods revealed that the "frondosa" condition was common throughout the area. The following year was characterized by moderate fertility in the tagged group of plants and no mixed fronds were observed. As mentioned earlier, in the cases studied by the writer, the sterile portion of the leaf was always basal, with the fertile pinnae more apical in location. Since the initiation of the pinnae along the rachis proceeds from base to apex (Steeves and Briggs, 1958), it is suggested that the leaves were originally determined as sterile fronds and then changed over to the fertile condition after pinna initiation had begun. In individual mixed pinnae, however, it is the basal portion which is fertile and the tip sterile; and the same is true of mixed pinnules. An explanation of this phenomenon cannot as yet be given since the development of pinnae is not known in sufficient detail.

In contrast to the form just discussed, *O. cinnamomea* f. *latipinnula* Blake is both striking in appearance and rare in occurrence. It was originally described by Blake in 1913 on the basis of its broad, deltoid pinnules which are characterized by a crenulate margin which may even become faintly lobed. The pinnules are reduced in number and are correspondingly broad (more than a centimeter in some cases). The venation is unusually coarse and the lateral veinlets are more pronounced than in normal fronds (fig. 1, cf A and B with C and D). In many ways the fronds are suggestive of juvenile leaves of the species except, of course, for size. Originally described from Vermont, f. *latipinnula* has subsequently been collected in Massachusetts (Report on the Flora of Massachusets II, 1933), Pennsylvania (Gruber, 1940) and New York.

In the early summer of 1951, three plants of f. *latipinnula* were found by the writer, growing through a pile of brush on

a powerline right-of-way in Hingham, Massachusetts. The identity of the material was established by Prof. W. H. Wagner, Jr., who also ascertained that there was no polyploidy involved in this unusual vegetative form. The fronds were late in emerging from the apical bud and were very slender and weak. Two of the abnormal plants were carefully marked, and a third was taken to the laboratory in the fall and stored over winter in a cold room. In the following spring, this plant was forced in a greenhouse. This plant, as well as the two left in the field, were of essentially normal form, although the fronds showed some slight deviation from the typical condition. In any event they were not of the *latipinnula* type. Clearly then f. *latipinnula* is a temporary condition representing a modification of normal leaf development.

It seemed at least possible that the heavy covering of brush had in some way induced these abnormal characteristics. Accordingly, in the fall of the year, several tagged normal plants were covered by similar piles of brush. These plants were examined in the following spring and found to be essentially normal. The fronds grew through the covering with difficulty, and were somewhat distorted; but they did not show the *latipinnula* characteristics. In late summer of 1951 a large-scale experiment was performed, to the writer's benefit but not at his instigation, which shed much more light upon the nature of this aberrant form. The powerline right-of-way was cleared again and new poles were set. These operations involved the bringing of considerable heavy equipment into the area. The following spring, a number of new examples of f. *latipinnula* were discovered in the cleared area. They were of the same form as the previous examples, but the fronds were not weak. Furthermore, there was no covering of brush over them.

There was now sufficient material available to make it possible to dissect some of the plants in an attempt to ascertain the cause of the abnormality. In all cases there was definite evidence of injury to the plant, and many leaf bases showed the results of breaking or crushing. Two plants, located side-by-side, were especially enlightening in this connection. Both were in the path

of a truck tire track, and both were of the *latipinnula* type. Examination of the plants which had been found during the previous season also gave clear evidence of injury, presumbly in an earlier clearing operation. It thus seemed reasonably established that the f. *latipinnula* is a response to rather drastic injury. It was, moreover, possible to establish the role which the injury had played.

Previous studies (Steeves and Wetmore, 1953, Steeves and Briggs, 1958) have shown that *O. cinnamomea* is characterized by a slow rate of leaf development. Leaves are produced at the shoot apex and develop within the apical bud for nearly four years before finally expanding above ground. As a consequence, the apical bud contains a large reservoir or pool of immature leaves, sufficient throughout most of the year for four subsequent growing seasons. During the growing season preceding final expansion of an annual set of fronds, the leaves of this set acquire the form of cataphylls (bud scales), fertile fronds and sterile fronds; and, starting from the outside of the bud, this is the sequence of leaf types within each set. Both fertile and sterile fronds form a rachis with pinnae, coiled into the characteristic fern crozier. The cataphylls, on the other hand, develop a flaring margin on the leaf base, but the portion which in the other leaves develops into the above-ground portion, is arrested in its growth and does not complete its development. During the winter, the cataphylls enclose and protect the apical bud. In the spring the fertile and sterile fronds push up inside these and expand above ground. Then a new set of cataphylls, fertile fronds and sterile fronds begins to take form from immature leaves inside these. Also, at the very center of the bud, a new set of primordia is added to the reservoir by the apical meristem. In other words, each year one set of leaves is used up at the outside of the bud and a new set is added at the center, so that the number of sets in the pool remains relatively constant. The cataphylls early lose any power to develop a complete rachis with pinnae because the leaf apex stops growing and usually undergoes necrosis. This loss progresses from the outside of the set inwards, but ends abruptly with the first frond, the apex of

which is actively developing. Early in the growing season, the removal of the current year's set of fronds has the effect of forcing some of the cataphylls to expand above ground. If this operation is performed somewhat later, the outer cataphylls will not respond, but some of the inner ones which have not lost the power of apical growth may do so. After early July, there is ordinarily no response at all; but sometimes a drastic treatment, such as complete mowing of a large area, will cause some of the innermost cataphylls, or even some of the next season's fronds, to complete their development and expand. Under these conditions, the fronds which emerge may be abnormal, and many show a broadening of the pinnae suggestive of the f. *latipinnula*. They are not, however, typical examples of this form.

In the case of the plants which showed *latipinnula* characteristics in 1952, the situation was somewhat more complex; but an examination of the cataphylls and persistent leaf bases outside the fronds of the current year has made an interpretation possible. In the latter part of July of 1951, the area was cleared and all fronds were mowed down. In many plants, probably including those under consideration, some of the inner cataphylls began to develop as fronds. The fronds for the next growing season continued to develop their croziers or a few may have started to form cataphylls. Then, later in the summer, an injury occurred which destroyed not only the released cataphylls, but also the fronds for the next growing season and possibly some leaves inside them. Subsequent developments are not very clear; but it appears that a new set of cataphylls was formed inside the crushed fronds, and that inside these a new set of fronds developed for the next season. In fact, the cataphylls and new fronds were, to a certain extent, intermixed, a condition never found in normal plants. When these new fronds expanded during the following spring they were of the *latipinnula* form.

In essence, the injury, occurring when it did, pushed the entire leaf utilization sequence considerably further into the special bud than is normal. The *latipinnula* fronds developed, therefore, much more rapidly than under normal circumstances. It is suggested that the drastic change of form of these fronds was

the result of this accelerated development. The tendency toward the *latipinnula* condition in fronds forced by mowing in late summer provides support for this interpretation. Changes in leaf form resulting from acceleration of development have been noted previously and have been described in detail in certain woody dicotyledons by Späth (1912). In any event, the f. *latipinnula*, like the f. *frondosa*, has no genetic or taxonomic significance, but should rather be regarded as one of the variable morphogenetic expressions of the leaf of *O. cinnamomea*.

It is a pleasure to acknowledge the valuable assistance of Mr. C. P. Steeves and Mr. G. S. Lord in making field observations and in reconstructing the history of the area in which they were made, and to Prof. W. H. Wagner, Jr. for his helpful advice and suggestions. Miss Barbara Coffin very kindly drew the illustrations in Fig. I. — DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATCHEWAN, SASKATOON, SASK.

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